A NEW DICYNODONT ANCESTOR FROM THE UPPER ECCA (LOWER MIDDLE PERMIAN) OF SOUTH AFRICA

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(With 13 figures in the text)

Contents

Introduction

The South African Karroo (Fig. 1) is well known for the abundance and variety of reptilian forms found in its bedded shales. Of the four major constituent series, viz. the Dwyka, the Ecca, the Beaufort and the Stormberg, the Beaufort Series has yielded the majority of fossils. The relative abundance and variety of forms found in the lowest layers of the Beaufort Series and the virtual total absence of fossil discoveries in the underlying Ecca Series led to the generally accepted view that the Ecca was barren.

This view was supported on tectonic evidence by many geologists, amongst them the noted South African geologist Alex du Toit (1948), who states that the absence of Lower Permian vertebrates, save fishes, from the deep and presumably cold-water geosynclinal deposits, such as the 'Green' or 'Blue Ecca' facies of the South African Cape Province or the 'Coal Measure' deltas and swamps to the north east, was understandable, for whereas tropical to subtropical climatic conditions would seem to have ruled in the Northern Hemisphere during Permo-Carboniferous times, the land in the Southern Hemisphere was still recovering from a great Ice Age. He maintained further that it was only during the later Permian that silting, coupled with the initiation of the Cape Fold Ranges within the geosyncline, produced shallowing. By intercepting moisture from the ocean to the south, the Fold Ranges would have reduced precipitation over the interior basin, the drier climate producing sediments of a more terrestrial nature which would have enabled tetrapods to enter the southern section of the hollow. This, according to Du Toit, was the reason for the abundance of new life during the Lower Beaufort in the southern and central Karroo region, in contrast to its scarcity, in equivalent horizons, further north.

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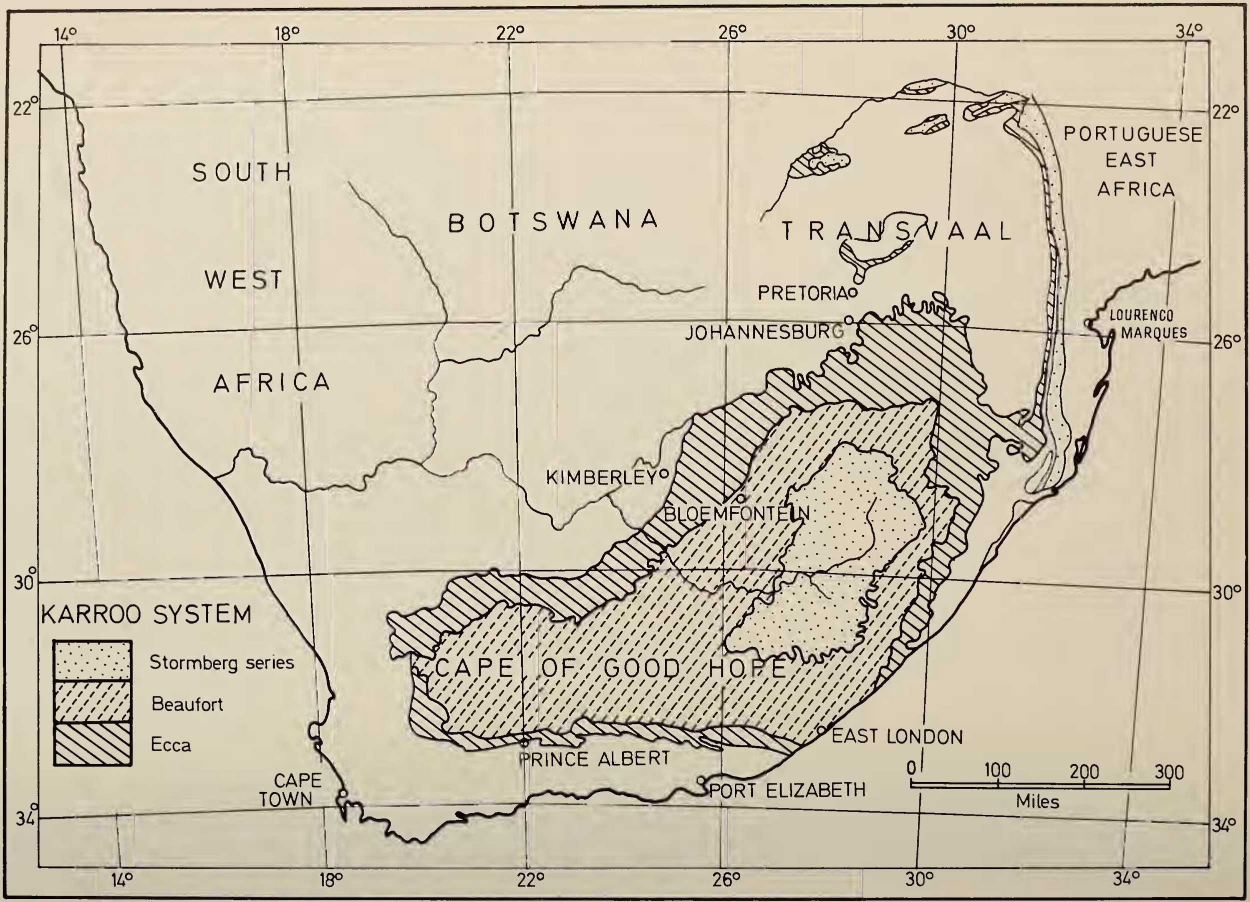

Fig. 1. Sketch map of the Karroo System.

The fact that Du Toit's views regarding the climatic conditions which prevailed during Ecca and Beaufort times were generally accepted by geologists and palaeontologists alike was probably a contributing factor why such scant attention was paid to Broom's claims that the terrestrial forms *Eccasaurus priscus* (Broom 1905*a*, 1912) and *Archaeosuchus cairncrossi* (Broom 1905*b*, 1909) came from Ecca beds. The announcement (Barry 1972) of the discovery by Mr Roy Oosthuizen of the farm Zwartskraal, Prince Albert district, of some 50 nodules containing fossil remains in beds which are Ecca (Lower Middle Permian) according to present stratigraphical definition, seemed to warrant the reopening of the 'barren Ecca' theory.

The southern or 'Green' facies in which the latest fossils were found was deposited within the Karroo Geosyncline. The strata occur south of a line drawn from Calvinia (latitude 31°30'S) in the west to East London (latitude 33°S) in the east, and range in thickness from 2 000 metres near Prince Albert to over 3 000 metres north of Grahamstown. The beds are involved in the Cape foldings and consist of green, bluish, olive and variegated mudstones and argillaceous sandstones and of a blue-green and yellow fine- to medium-grained hard and sometimes quartzitic spheroidally-weathering sandstones, but without any coarse or conglomeratic kinds.

Because of the Cape folding the strata are in places tilted up vertically and even overturned towards the north as between Prince Albert and Klipplaat (Du Toit 1954). Duplication of exposures of the same beds are commonly found, thus complicating the determination of fossil horizons, but on site investigations of the layers and folding patterns at Zwartskraal show the fossil sites to lie within the Upper Ecca (Figs 2 and 3). Lower Beaufort exposure is limited to a narrow projection eastwards along the Sandriver valley with the fossils occurring to the north, south and east of this exposure.

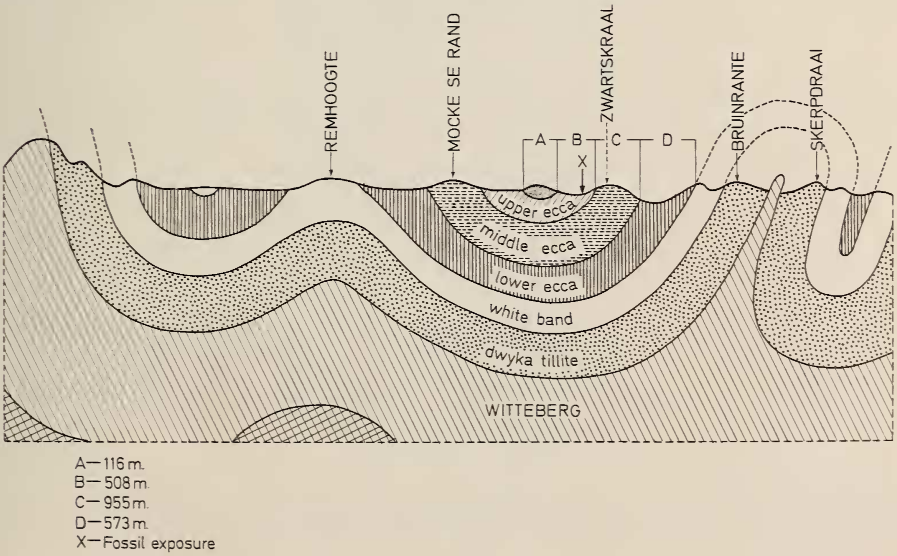

Fig. 2. Cross-section of the strata at Zwartskraal, Prince Albert.

As mentioned earlier, the first major deposits of reptilian fossils in the South African Karroo system occur in the *Tapinocephalus* zone of the Beaufort Series. This fauna is rich in numbers and established genera and already displays a diversified and balanced ecological composition (Boonstra 1969). Considering this, and the fact that the lithology does not show a sudden transition between the underlying Ecca and the Lower Beaufort, Barry (1972) contended that these factors were not consistent with the generally held view that climatic conditions during Upper Ecca times were such that they mitigated against the existence of land vertebrates during this period.

This view would seem to be borne out by comparative osteological studies carried out on the fossil material which forms the subject of this paper.

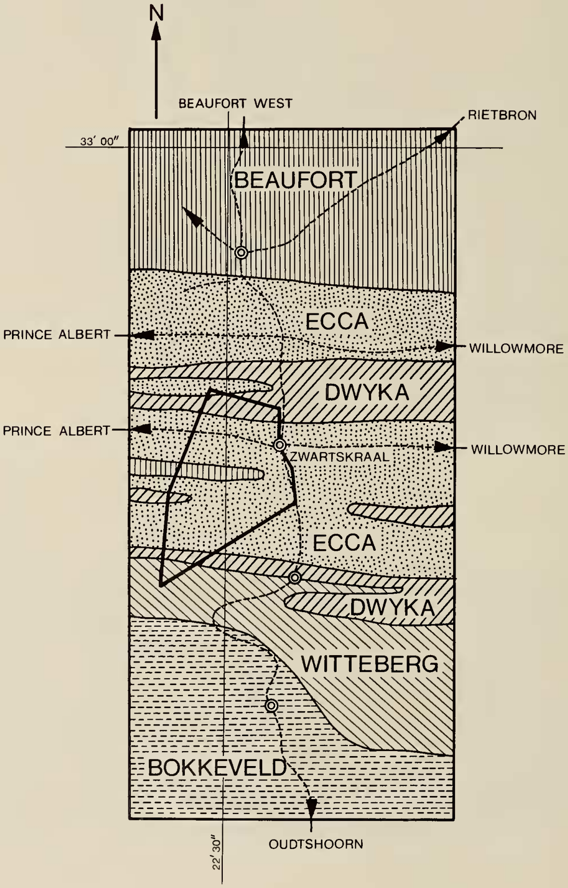

Fig 3. Geological map of the Zwartskraal area.

STRATIGRAPHIC AND LOCALITY DATA

Eodicynodon oosthuizeni and other specimens still to be described came from Mr Roy Oosthuizen's farm Zwartskraal in the Prince Albert District of the Cape Province, Republic of South Africa, and were collected by him between 1964 and 1970. A schematic cross-section of the area in which the fossil was found is shown in Figure 2.

The Zwartskraal material found to date includes the following:

(1) the skull of a new species, designated *Eodicynodon oosthuizeni*
(2) portion of a basicranial axis
(3) the skull of a small dicynodontid
(4) the palate, quadrate and articular of a small endothiodontid
(5) eroded skull of a small dicynodontid
(6) postcranial skeleton of small therapsid
(7) snout of small dicynodontid
(8) many small unidentifiable pieces

With the exception of specimen no. 3, which was sectioned using the Croft Parallel Grinding method, all specimens were acid prepared using weak formic acid to remove the matrix.

SYSTEMATICS

Class **REPTILIA**
Order THERAPSIDA
Suborder **ANOMODONTIA**
Infra-Order DICYNODONTIA
Family **Dicynodontidae**
Sub-Family Dicynodontinae

Eodicynodon gen. nov.

Diagnosis: Skull small, *Dicynodon*-like in skull form and possession of a pair of canine tusks, but showing ancestral features. Vomers paired, lateral pterygoid processes strongly developed, premaxillaries partly paired.

Eodicynodon oosthuizeni sp. nov.

Holotype: Skull lacking anterior portion of snout and mandible. R.O.Z. No. 1 (collection of Mr Roy Oosthuizen).

Horizon and locality: Upper Ecca (Lower Middle Permian), Zwartskraal, Prince Albert District, Cape Province, Republic of South Africa.

Diagnosis: Same as for the genus.

CRANIAL OSTEOLOGY

The skull lacks the mandible, the right temporal arch and the anterior portion of the snout (Figs 4 and 5). For an unknown reason the latter is a feature common to all of the skulls found to date. Because of this, few longitudinal measurements could be taken but of these the ratio 'anterior limit of the squamosal to pineal'/'pineal to anterior limit of orbit' would seem to be of some significance. In *Eodicynodon* this is 1 : 3,6, compared with 1 : 1 or an outside limit of 1 : 2 ratio in all *Dicynodon* species measured. It is of interest to note that nearest ratio in the Dicynodontia would seem to be the 1 : 4 ratio of *Lystrosaurus*.

The interorbital width is less than the intertemporal width, giving a ratio of 3 : 4. The postorbital is broad, sloping ventro-laterally at an angle of 35° to the top of the skull roof. The parietal becomes slightly narrower posteriorly, a postero-laterally directed flange extending posteriorly well beyond the medial termination of the bone.

Fig. 4. *Eodicynodon oosthuizeni*, dorsal view.

Fig. 5. *Eodicynodon oosthuizeni*, ventral view.

The pineal foramen is oval-shaped and situated on a slightly raised triangular platform (Fig. 6). The surface of the platform, and especially the V-shaped portion extending posteriorly from the rim of the pineal, is rugose. The rim itself projects above the platform.

A posteriorly directed process of the frontal reaches a point in line with the front of the pineal foramen. The postfrontal lies lateral to this process. The parietal is well developed, an anteriorly extending process reaching the level of the postorbital arch. The medianly situated preparietal is wedged in between the frontals and parietals, the frontals meeting its anterior and anterolateral borders.

Although the configuration of most of the dermal bones of the skull roof would seem to resemble that of the genus *Dicynodon*, the preparietal does not participate in the formation of the rim of the pineal foramen, as is generally found in *Dicynodon* species. In *Eodicynodon* it lies 3 mm in front of the foramen, a distinct suture indicating the line along which the parietals meet anterior to the pineal foramen to separate the preparietal from the pineal foramen.

Although both Broom (1935) and Toerien (1953) have considered the relationship between the pineal foramen and the preparietal, it would seem advisable to re-analyse the position in the light of conditions found in *Eodicynodon*. Broom (1935: 7) found that in *Dicynodon grimbeeki* 'The pineal foramen is rather small and rounded and behind it a little median boss of bone. The preparietal lies in front of the pineal, but on the surface at least it it covered by the parietal, so that the posterior end of the preparietal is 3,5 mm in front of the foramen. A second skull has a similar condition. In one of the male skulls the preparietal nearly reaches the pineal. In others the preparietal forms the anterior wall of the foramen. In some of these the bone is a little weathered, and possibly a bridge of the parietal in front of the foramen has been weathered off. In the type skull the parietal forms the surface bone in front of the foramen, but it sends forward a process on each side of the preparietal.' Toerien (1953: 54) re-examined Broom's material and states that he found this deviation from the

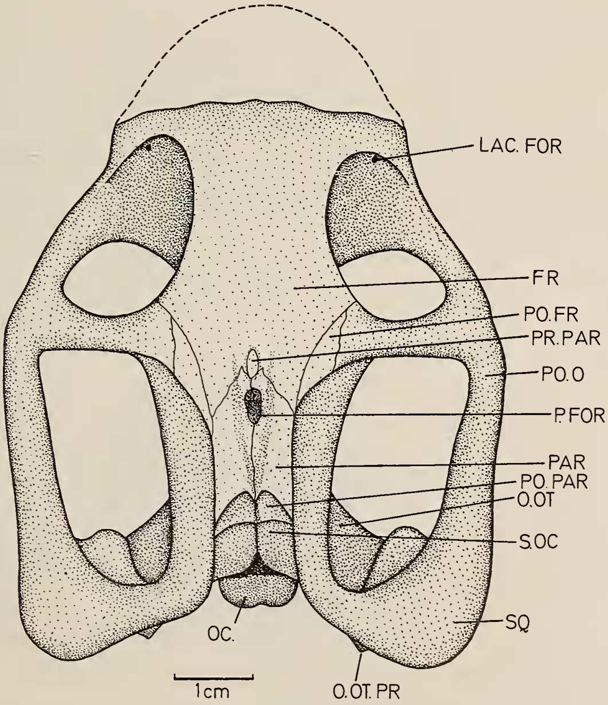

Fig. 6. *Eodicynodon oosthuizeni*, dorsal view.

general dicynodont condition to be the case in only 4 specimens of *D. grimbeeki*, including the type, and concluded that the non-participation of the preparietal in the formation of the pineal foramen 'is a rare feature in Dicynodons, but is not uncommon in some of the small Endothiodonts'.

Phylogenetically the preparietal makes its first appearance in the therapsids. Even amongst them it is not universally present but confined to the Gorgonopsia and Dicynodontia. Huxley (1865: 10) was the first to describe this '. . . undivided bone wedged in anteriorly between the two parietals' in a skull fragment from the Panchet Rocks in Bengal. He identified the fragment as belonging to the genus *Dicynodon* on the strength that in a specimen of *Dicynodon murrayi* and in *D. lacerticeps*, '. . . while the two parietal bones are separated by a median suture a single intercalary, or wormian, bone is interposed between them and the frontals, and bounds the parietal foramen, in just the same way as the single median bone limits it in the Indian fossil' (p. 11). Seeley (1895) appears to be the first worker to have referred to this bone as the preparietal.

The preparietal retains a fairly constant position at the median intersection of the frontals and parietals which would seem to be commensurate with its identification as a 'Wormian bone'. Its relationship with the pineal foramen, which in both the ancestral Pelycosauria and Cotylosauria retains a fairly constant position well inside the borders of the parietals, is variable within the Gorgonopsia and the Dicynodontia.

In the majority of the Gorgonopsia the preparietal occupies a position anterior to the pineal foramen. The exceptions to the rule include *Aloposaurus ?tenuis* from the *Cistecephalus* zone in which 'le grand preparietal touche l'orifice pineal' (Sigogneau 1970: 111) and forms such as *Sycosaurus laticeps* (Haughton 1924), *Sycosaurus brodiei* (Broom 1941) and *Leontocephalus cadlei* (Broom 1940) similarly from the *Cistecephalus* zone, in which the preparietal is entirely absent. Sigogneau (1970) has interpreted this latter condition as secondary.

In the majority of Dicynodontia again, the preparietal is closely associated with the pineal foramen, participating to a lesser or larger degree in the formation of the rim of the foramen. The exceptions here include the Ecca form *Eodicynodon*, the *Endothiodon* zone forms *Emydops arctatus* (Owen 1876), *Emydops longus* (Broom 1921), *Emyduranus platyops* (Broom 1921), *Emyduranus granilis* (Broom 1936), *Emydorhynchus formosus* (Broom 1936), and the *Cistecephalus* zone form *Emydorhinus sciuroides* (Broom 1921), in all of which the preparietal lies anterior to the pineal foramen. In what is considered to be a secondary condition the preparietal increases its participation in the formation of the borders of the pineal foramen. This trend is illustrated in *Diictodon galeops* (Broom 1913), *Aulacephalodon peavoti* (Broom 1921) and *Aulacephalodon tigriceps* (Broom 1932), all from the *Cistecephalus* zone in which the hind portion of the preparietal very nearly or completely surrounds the foramen. In others such as the genera *Cistecephalus* and *Myosauroides minnaari* (Broom 1941) from the *Cistecephalus* zone the preparietal is entirely absent.

Thus, in the Dicynodontia as in the Gorgonopsia, the primary position of the preparietal would seem to be the one in which the preparietal is situated anterior to the pineal foramen. The increased participation of the bone in the formation of the borders of the pineal foramen in some forms and its absence in others can be considered to be stages in the later development of the skull roof.

Judging by its relationships with surrounding elements it would seem certain that the pineal foramen retains a fairly constant position in the skull roof and that it is the preparietal which is subject to backward displacement. In forms such as *Dicynodon woodwardi* (Broom 1921), *Aulacephalodon peavoti* (Broom 1921) and *Aulacephalodon haughtoni* (Broom 1921), all from the *Cistecephalus* zone, this backward movement would seem to be accompanied by an increase in the relative size of the preparietal.

The postparietal(s?) occupies the dorsomedial area of the slanting occipital plate (Fig. 13). The name postparietal is here preferred to that of interparietal, usually used, as the bone is not situated between the parietals in this form. It also differs significantly from the usual dicynodont condition in that a medial postero-ventrally directed longitudinal ridge divides the bone into bilateral concave elements. The longitudinal ridge shows a pronounced midline groove or cleft extending the length of the bone. It is not possible to see whether this represents an entire or partial separation of the postparietal into two elements, but it would seem to reflect the ancestral paired condition of this element as found in *Captorhinus* and other cotylosaurs.

It is interesting to note that the postparietal is single in most pelycosaurs (Romer & Price 1940: 50). Although a well-developed ridge is absent, a longitudinal mound in the midline separates the concave areas on its sides. In most known Gorgonopsia the bone is also single but the median ridge is prominent, extending even on to the supraoccipital, the concavities following the general outward sweep of the tabulars and squamosals.

As mentioned earlier, the front portion of the snout has been eroded away.

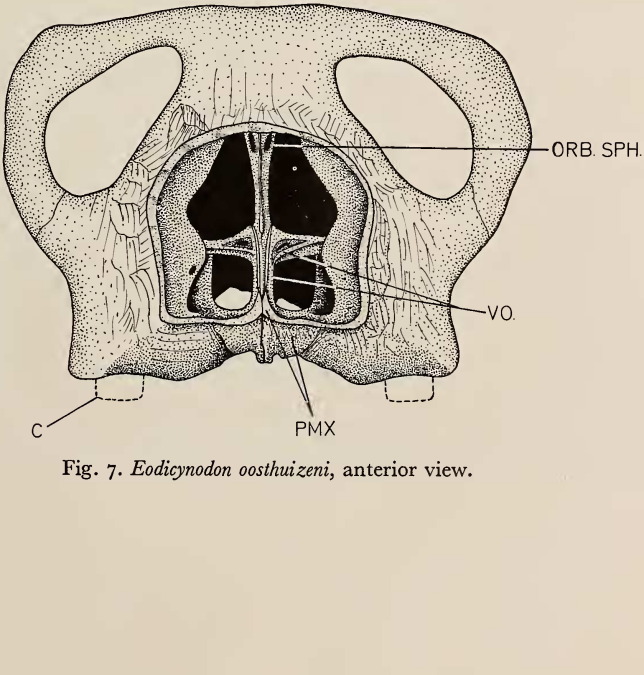

Fig. 7. *Eodicynodon oosthuizeni*, anterior view.

However, part of the premaxillary is still present and shows signs of being paired. A hairline suture extends the length of the palatal face of the bone and is seen to continue dorsally into the short dorsally directed median process of the premaxillary (Figs 7 and 8). The two relatively thin plates thus formed represent the single dorsal premaxillary process commonly found in *Dicynodon*.

Paired premaxillaries are not known in any other member of the Dicynodontia. Its presence in the presumably related, but primitive, Russian forms *Venyukovia* and *Otsheria* and in the sphenacodont Pelycosauria would seem to point to the fact that the paired condition in *Eodicynodon* represents the ancestral condition. The fusion of the premaxillaries in all Beaufort Series Dicynodontia is a secondary evolutionary trend which has not been followed by the other synapsid groups.

The premaxillary ends postero-medially in a short palatal process which makes contact with the vomer (Fig. 8). A postero-laterally directed tapering extension continues some distance backward so that the premaxillary forms the anterior and antero-lateral borders of the choana. The presence in Pelycosauria of a similar relationship would seem to point to a primitive condition, for in later dicynodonts the palatal face of the premaxillary increases in size thereby pushing the choanae further back. *Robertia broomiana*, a small endothiodont from the lowest division of the *Tapinocephalus*, which Toerien (1953) suggests is the most likely ancestor of *Oudenodon*, shows close resemblance to the *Eodicynodon* condition with the difference that, although the secondary palate is still short and the internal nares reach the level of the tusks, the anterior parts of the choanae are reduced to slits and therefore open functionally more posteriorly. In *Eodicynodon* the functional anterior limit of the choana lies in line with the canine tusk. Within the nasal cavity there is a longitudinal groove on either side of the median premaxillary septum which leads to the anterior notch of the choana. Camp & Wells (1956) suggested that a similar groove found in *Placerias* served to transmit the duct of Jacobson's organ. A similar groove is found in *Lystrosaurus* (Cluver 1971).

Due to a pronounced overlap of the ventro-lateral portion of the palatal surface of the premaxillary by the maxillary the palatal surface of the former shows as relatively narrow (Fig. 8). In later dicynodonts such as *D. grimbeeki*, *Pristerodon buffaloensis*, etc., this relationship is reversed, the lateral border of the premaxillary lying ventral to the maxillary. The condition in *Eodicynodon* seems to be a retention of the pelycosaurian condition as in the latter the premaxillary is 'deeply overlapped by the maxilla' (Romer & Price 1940: 54). The increased contribution of the premaxillary to the composition of the secondary palate as seen in later dicynodonts would thus necessitate the development of a new premaxillary process covering the maxillary from below.

In all known dicynodonts the vomer is a median unpaired sheet of bone, bifurcated anteriorly and posteriorly. One of the most important features distinguishing *E. oosthuizeni* from other dicynodonts is that the vomer is distinctly paired in this species (Fig. 8). Anteriorly the vomers form the inter-

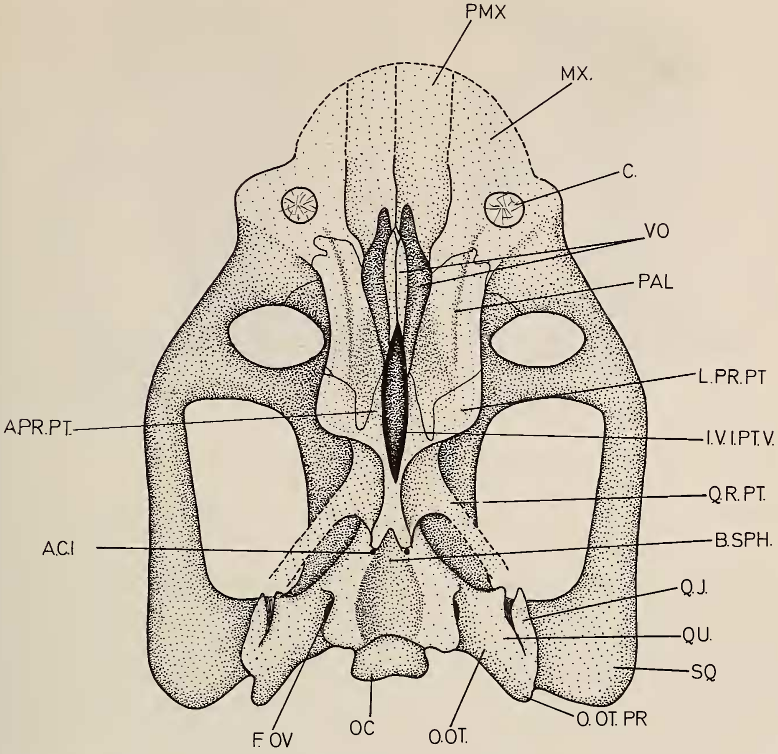

Fig. 8. *Eodicynodon oosthuizeni*, ventral view.

digitating contact with the premaxillaries as seen in *Pristerodon* (Barry 1967) but behind this area the palatal surface of the anterior third of the vomers is a pair of relatively broad, rounded ridges. Immediately behind this region the vomers curve upwards above the general palatal level of the palate, and the ridges now become thin and blade-like with a V-shaped groove developing between them. In this way the vomers form the anterior and antero-lateral borders of the interpterygoidal vacuity. As vomeral elements participate in the formation of the boundaries of this vacuity, the interpterygoidal vacuity in *Eodicynodon* technically becomes an intervomero-interpterygoidal vacuity (Fig. 8). This is also the case in most dicynodonts. In many *Tapinocephalus* zone dicynodonts the vomers form more than one half of the borders of the intervomero-interpterygoidal vacuity. The evolutionary development leading up to this condition has been dealt with in a separate paper (Barry, in press).

The vomers are continued dorsally to form a paired median septal sheet. Dorsally each half of this paired sheet flares out laterally in a horizontal plane, thus forming the median and dorsal walls of the internal nares. It is in contact laterally with the palatine and posteriorly with the pterygoid.

Fig. 9. *Eodicynodon oosthuizeni,* stereoview.

Paired vomers reflect the primitive tetrapod condition, being present not only in sphenacodont pelycosaurs but also in the captorhinomorph cotylosaurs. The paired condition has also been recorded for the Russian Zone II form *Venyukovia* (Efremov 1940) which according to Watson (1948) occupies a position between the Dinocephalia, which similarly retain paired vomers, and Dicynodontia, in which the vomers have become fused. It is of interest to note that the vomers have become secondarily fused in only two of the main groups of the Therapsida, viz. the Dicynodontia and Gorgonopsia.

The palatine is developed along two planes; a rugose ventral, comparatively broad kidney-shaped section extending along the general palatal line from just behind the canine tusk to a tapering point in line with the anterior limit of the inter-pterygoidal vacuity, and a dorso-medially curving section which meets the dorso-lateral flange of the vomer to form the lateral and dorsal walls of the internal nares (Fig. 8). Postero-medially the palatine meets the pterygoid in a long suture.

The ectopterygoid forms part of the outer edge of the palate and is wedged between the pterygoid, palatine and maxillary. Its ventral surface is as rugose as that of the palatine, from which it is separated by a deep longitudinal groove.

The rugosity of the ventral surfaces of the ectopterygoid and palatine could possibly be related to the clusters of small teeth on corresponding areas on the palatine, pterygoid and ectopterygoid in pelycosaurs such as *Dimetrodon* and *Edaphosaurus.* In *Eodicynodon,* the antero-ventral portion of the vomer is similarly covered with small ring-like protuberances resembling the small vomerine teeth in *Edaphosaurus.* In most gorgonopsians sparse clusters of small teeth occur on the palatine and pterygoid.

The pterygoid has 3 main processes extending from the median plate, viz. the anteriorly directed palatal ramus, the laterally directed lateral process and the postero-laterally directed quadrate ramus of the pterygoid. Postero-medially the pterygoid meets the parabasisphenoid. As in other dicynodonts the pterygoid bears no teeth.

In Pelycosauria, the pterygoid possesses a long anterior process running horizontally in the palate to meet the vomer. The process meets its mate along their entire length. The anterior process has undergone a drastic reduction in length in *Otsheria* and *Venyukovia* but the processes still meet in the midline anterior to the interpterygoidal vacuity and before making contact with the vomer. In *Eodicynodon* as in all other dicynodonts the anterior processes do not meet in the midline but are separated to form the postero-lateral walls of the intervomero-interpterygoidal vacuity (Fig. 8). As shown elsewhere (Barry, in press) this development is not restricted to the dicynodont line but is also evident in the Dinocephalia.

In the region of the intervomero-interpterygoidal vacuity the pterygoid sends out a broad ventro-lateral projection, the lateral process (Figs 8 and 10). As the lateral process is strongly developed in the pelycosaurs and is absent in dicynodonts, it would seem to indicate the retention in *Eodicynodon* of a primitive character. *Otsheria* still shows a prominent lateral process but it is less well developed in *Venyukovia*.

The basicranial axis of *Eodicynodon* consists of the basioccipital, the basisphenoid and the dermal parasphenoid which is fused with the latter (Figs 10 and 11). The median sphenethmoid complex is situated anterodorsally to the parabasisphenoid. The paired carotid arteries enter the basisphenoid ventrally and emerge dorsally through a single canal posterior to the base of the parabasisphenoid rostrum (Fig. 12). Unfortunately the proximal portion of the parabasisphenoid rostrum is missing so that it is not possible to determine

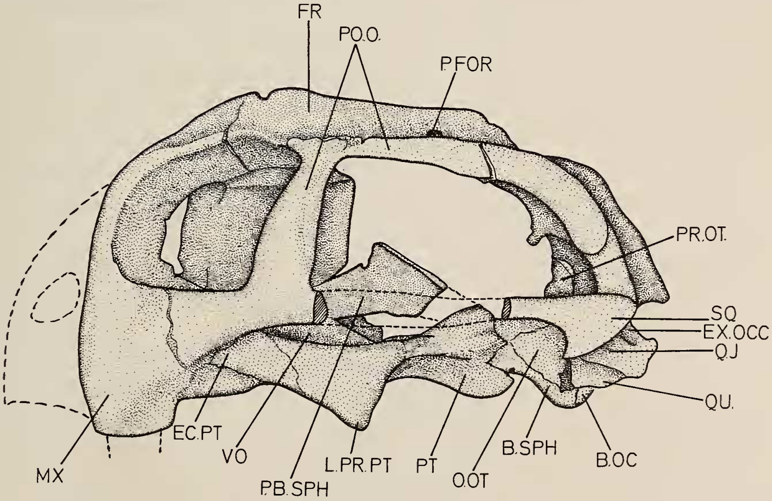

Fig. 10. *Eodicynodon oosthuizeni*, lateral view, left side.

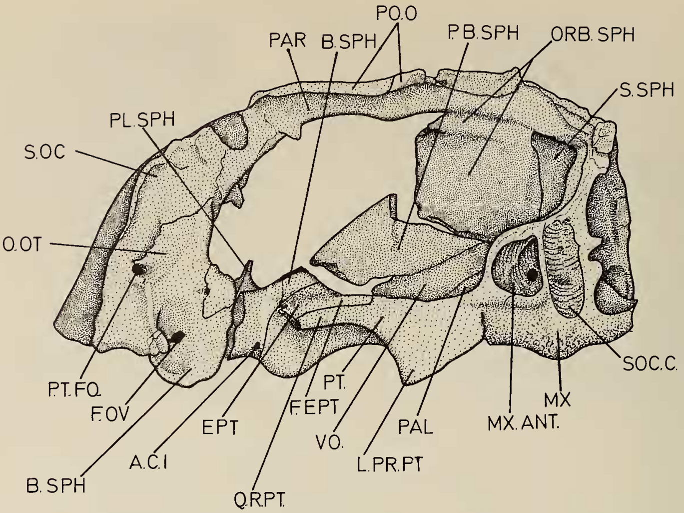

Fig. 11. *Eodicynodon oosthuizeni*, lateral view, right side.

whether the basisphenoid and parasphenoid are indistinguishably fused throughout its length as would seem to be the case in dicynodonts and also in the pelycosaurs (Romer & Price 1940).

The parabasisphenoid arches upwards and forwards at an angle of 45° before levelling off to run parallel to the main axis of the skull. A short distance behind the interorbital plate the dorsal portion of the bone ends abruptly as if it butted against an unossified posterior portion of the interorbital plate (Fig. 11). It is not clear from the specimen whether the dorsal portion of the parabasisphenoid must be regarded as a dorsal process of the parabasisphenoid rostrum, whether it represents a separate septal ossification (the so-called presphenoid claimed for most dicynodonts), or whether it is an anterior extension of the basisphenoid within the parabasisphenoid rostrum. Although there is no sutural evidence of dorsal and ventral elements in the parabasisphenoid in *Eodicynodon* this possibly cannot be ruled out. Near similar conditions are found in pelycosaurs where according to Romer & Price (1940: 76) '. . . in some cases the basisphenoid terminates abruptly within the parasphenoid trough . . .' just behind the posterior end of the orbitosphenoid. Barry (1967) found questionable indications in *Pristerodon* of a suture dividing the rostrum horizontally and states that the shape of the posterior part of the rostrum lends support to the conclusion that it consists of two fused elements, the rostrum parasphenoidale ventrally and either a rostrum basisphenoidale or rostrum praesphenoidale dorsally. The latter alternative depends upon whether the ossification in the trabecula communis represents an extension anteriorly into the trabeculae of the ossification of the basisphenoid or whether it is a separate ossification in the trabecula communis. It can also be pointed out that amongst recent reptiles, lizards have a rostrum parasphenoidale while *Chelone* has a rostrum basisphenoidale. Judging by the flatness and slightly roughened condition of the dorsal surface of this process it would seem possible that the braincase wall was continued by cartilage above this point (Fig. 10).

Anterior to this process, the dorsal surface of the parabasisphenoid rostrum, which probably now represents parasphenoidal elements only, is deeply grooved to accommodate the lower end of the interorbital plate. Approximately halfway along the ventral border of the plate, the upwardly expanded median sides of the vomer take over the function of providing a groove for the plate (Fig. 11). It is not certain how far anteriorly the parasphenoid rostrum continues within the trough formed by the vomers.

The interorbital plate is roughly rectangular in shape and extends anteriorly from a point in line with the postorbital bar to the anterior rim of the orbit (Fig. 11). There are definite indications that the plate consists of two median ossifications separated by a vertical division. The homology of the elements comprising the sphenethnoid complex and the terminology used by different authors varies considerably and has been dealt with by Barry (1967) and Cluver (1971). For reasons set out previously (Barry 1967), the posterior of these two ossifications will be referred to as the orbitosphenoid and the anterior ossification as the septosphenoid.

The median keel of the orbitosphenoid is roughly square in outline. Dorsally it bears two concave lateral wings which dorsally make contact with the longitudinal ridges on the inner surfaces of the frontals. The median longitudinal trough thus formed is not subdivided by bone. The trough ends anteriorly at the front margin of the orbitosphenoid. From this point forward, at least, the brain must have been subdivided to form the olfactory lobes as the median septosphenoid extends upwards beyond the level of the trough before expanding laterally to form two narrow, slightly convex wings. The latter projections probably covered the olfactory lobes from above.

The palato-quadrate complex in dicynodonts comprises two separated bones, viz. the quadrate, with its two ventrally directed limbs which form the medial and lateral condyles, and the epipterygoid. The latter is usually L-shaped, a thin, dorsally projecting columella, rising from a footplate which rests upon and partly covers the dorsal surface of the quadrate ramus of the pterygoid.

In *Eodicynodon*, the lateral condyle of the quadrate and part of the medial one have been eroded away, but in spite of this the quadrate does not appear to have marked differences from the general dicynodont condition. It is not clear whether the quadratojugal participates in the formation of the lateral condyle.

The epipterygoid is unusual in that its base or footplate is more expanded than in dicynodonts in general. As can be seen in Figure 11 the footplate extends from a point in line with the posterior surface of the dorsal wing of the vomer to the root of the quadrate ramus of the pterygoid where it covers more than half the dorsal surface of the quadrate ramus of the pterygoid. Unfortunately the latter is broken off so that it is impossible to determine the length of the quadrate ramus of the epipterygoid but judging by its breadth at the break it could have

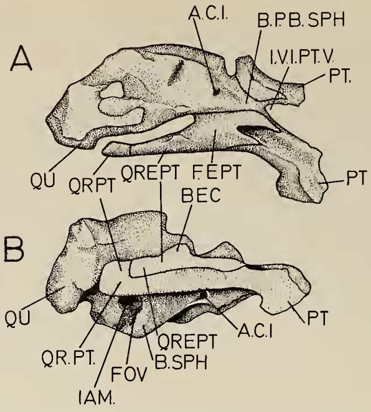

Fig. 12. *Eodicynodon oosthuizeni*, A. Dorsal view. B. Lateral view of palatoquadrate complex.

continued some distance posteriorly. At the break, the quadrate ramus of the epipterygoid has a distinct dorsally directed ridge, which probably represents the basal portion of the dorsally directed columella of the epipterygoid. A separate skull fragment featuring the basicranial axis confirms this view (Fig. 12).

Anterior to the base of the columella the footplate shows a broad medial expansion which stretches across the dorsal surface of the pterygoid and ends medially against the base of the parabasisphenoid (Fig. 12). The exceptional development of this part of the footplate of the epipterygoid is most unusual for dicynodonts. In the latter the footplate is only weakly developed, or not at all, and the columella is anterior to the base of the columella. In *Kannemeyeria* (Case 1934) and *Daptocephalus* (Ewer 1961) the footplate is continued anteriorly but as a much less extensive and narrower bone. Ewer (1961) suggested that this extension was possibly developed to compensate for the weakening of the middle region of the skull resulting from the narrowing of the parietal region. This interpretation does not hold true for *Eodicynodon* as the parietal region is relatively broad in this form. Being a dicynodont ancestor it is more likely that *Eodicynodon* would display the more primitive condition. The remarkable similarity of the *Eodicynodon* and *Dimetrodon* (Romer & Price 1940) footplates would seem to justify this conclusion. The anterior process found in *Daptocephalus* represents the retention in this form of a primitive feature rather than a later development. In all known Gorgonopsia too the epipterygoid still retains a long tapering anterior extension.

As in *Pristerodon* (Barry 1967) a well-demarcated groove is formed between the quadrate and quadratojugal, the latter being attached only at its ventral and dorsal extremities.

The occiput (Fig. 13) resembles a trapezoid with the oblique sides bowed gently outward. The cartilage bones of the region do not show many differences

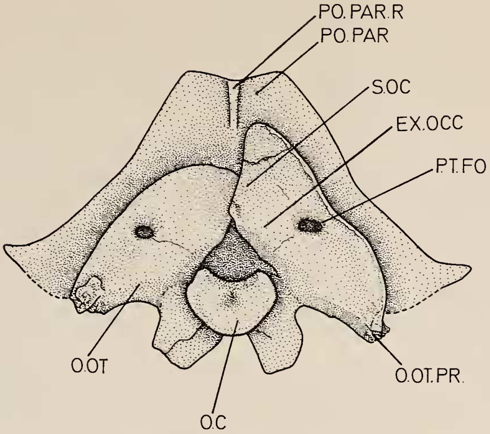

Fig. 13. *Eodicynodon oosthuizeni*. Occipital view.

from the general *Dicynodon* condition. The borders of the supraoccipital are only faintly recognizable but it would seem that its ventro-medial border forms the dorsal rim of the foramen magnum in the usual way. From here it fans out dorsally and laterally to meet the postparietal and tabulars.

The line of fusion between the supraoccipital and exoccipital cannot be traced. The exoccipital forms the lateral rim of the foramen magnum and extends outward to the post-temporal fossa. From its base a flat roughly triangular flange extends to cover the ventro-medial portion of the opisthotic. Although the sutures are indistinct it seems that the exoccipitals also form the lateral borders of the foramen magnum. The basioccipital forms the ventro-medial portion of the occipital condyle, it is continued anteriorly in the midline from where two ventro-laterally directed triangular extensions develop to cover the posterior surface of the prominent tubera, which form the bony casing of the fenestra ovalis and for the cochlear recess of the internal ear. In most dicynodonts the tubera are described as being formed by the basioccipitals, but in *Eodicynodon* each structure is quite clearly formed by the basioccipital and the basisphenoid, with the opisthotic forming the postero-lateral rim.

The opisthotic, similarly, is a roughly triangular plate. Its dorsal boundary extends from the ventro-lateral corner of the foramen magnum to the ventral rim of the post-temporal fossa. A ventro-medially directed flange forms the postero-dorso-lateral rim of the prominent tuber. As in *Pristerodon* (Barry 1967) the opisthotic carries a strongly developed ridge-like opisthotic process which laterally tapers into a posteriorly directed point (Fig. 13). As stated in the aforementioned paper it is believed that this process is associated with the origin of the m. obliquus capitis below it, and the m. rectus capitis posterior lateralis et medialis dorso-medially to it, as still found in some of the recent turtles in which an analogous process occurs.

The post-temporal fossa is small, as in *Tapinocephalus* zone dicynodonts.

The reduction in its size, in comparison with ancestral tetrapods, appears to be due to an increase in the size of the opisthotic. The reduction in size of the post-temporal fenestra would give support to the views of Watson (1911, 1913), Cox (1959) and Cluver (1971) that the fenestra probably served as a passage for the v. capitis dorsalis, which in modern reptiles such as *Sphenodon* drains the occipital musculature and passes forward to enter the braincase in front of the auditory capsule. In *Eodicynodon* a shallow, antero-dorsally directed groove on the pro-otic could indicate the passage of the vein within the braincase. However, a second shallow groove-like depression on the pro-otic, similarly emanating from the post-temporal fenestra, runs antero-medially along the surface of the pro-otic. The latter groove and the general smoothness of the bone anteriorly and antero-laterally to the inside edge of the fenestra suggest that in the ancestral forms, with its wide fenestra, and possibly still in *Eodicynodon*, other elements apart from the v. capitis dorsalis passed through the fenestra.

Summary

Unlike the *Tapinocephalus* zone (Lower Beaufort) beds of South Africa, which have yielded an abundance of diversified terrestrial forms, the Ecca beds which underlie them were considered to be devoid of such remains. This assumption was based on the view that these layers were deposited during a time when deep water conditions prevailed in the Karroo. It was strengthened by the fact that apart from two claims made by Broom, which were refuted, no terrestrial remains had been definitely reported from these beds.

The discovery, from 1964 to 1970, of a number of skulls and vertebrae of dicynodont-like animals in Ecca defined beds, reported during the 2nd International Gondwana Symposium (Barry 1972) resulted in the reappraisal of this view. Comparative osteological studies of the skulls show that they predate the *Tapinocephalus* zone forms in the retention of primitive features such as paired vomers, paired premaxillaries and the retention of the lateral processes of the pterygoid. These features are reminiscent of the Pelycosauria but have disappeared in the Lower Beaufort forms.

Eodicynodon has proved to be more primitive than any known dicynodont from the *Tapinocephalus* zone. On the other hand it shows so many typically dicynodont features that it cannot be excluded from the direct ancestry of at least some branches of the *Tapinocephalus* zone dicynodonts.

The affinities and systematic position of *Eodicynodon* formed the subject of a paper presented to the 3rd International Gondwana Symposium. It is scheduled to appear in 1974.

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Abbreviations

A.C.I.	Arteria carotis interna	ORB.SPH.	Orbitosphenoid
A.PR.PT.	Anterior process of the pterygoid	PAL.	Palatine
		PAR.	Parietal
B.E.C.	Base of the epipterygoid columella	P.B.SPH.	Parabasisphenoid
		P.FOR.	Pineal foramen
B.OC.	Basioccipital	PL.SPH.	Pleurosphenoid
B.P.B.SPH.	Base of the parabasisphenoid	P.MX.	Premaxillary
B.SPH.	Basisphenoid	PO.FR.	Postfrontal
C.	Canine tusk	PO.O.	Postorbital
EC.PT.	Ectopterygoid	PO.PAR.	Postparietal
EPT.	Epipterygoid	PO.PAR.R.	Post parietal ridge
EX.OCC.	Exoccipital	PR.OT.	Prootic
F.EPT.	Footplate of the epipterygoid	PR.PAR.	Preparietal
F.OV.	Fenestra ovalis	PT.	Pterygoid
FR.	Frontal	P.T.FO.	Posttemporal fossa
I.A.M.	Internal auditory meatus	Q.J.	Quadratojugal
I.V.I.PT.B	Intervomero-interpterygoidal vacuity	Q.R.EPT.	Quadrate ramus of the epipterygoid
LAC.FOR.	Lacrymal foramen	Q.R.PT.	Quadrate ramus of the pterygoid
L.PR.PT.	Lateral process of the pterygoid		
MX.	Maxillary	QU.	Quadrate
MX.ANT.	Maxillary antrum	S.OC.	Supra-occipital
O.C.	Occipital condyle	SOC.C.T.	Socket of the canine tusk
O.OT.	Opisthotic	S.Q.	Squamosal
O.OT.PR.	Opisthotic process	VO.	Vomer